SUCTION FEEDING IN BEAKED WHALES: MORPHOLOGICAL AND OBSERVATIONAL EVIDENCE

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ABSTRACT. Beaked whales possess several unique morphological features of the head. In most species, females and juveniles lack erupted teeth; the erupted teeth of adult males are used primarily for intraspecific fighting. All beaked whales possess one pair of throat grooves. Several authors have hypothesized that some toothed whales may capture prey primarily by suction. To test this hypothesis, we dissected a series of beaked whales and other cetaceans to ascertain the functional morphology related to this mode of feeding. The throat grooves of beaked whales allow for expansion of the gular region. A layer of loose connective tissue between muscle groups in the floor of the mouth allows the tongue to move freely as it is retracted posteriorly by the contractions of the *hyoglossus* and *styloglossus* muscles. The combined effects of tongue retraction and gular floor distention appear to function to create a sudden drop in intraoral pressure allowing beaked whales to suck in prey items. The relatively large hyoid bones provide the origin for several large gular muscles that control the tongue and the floor of the mouth. Observations of live animals corroborate the anatomical findings that beaked whales use suction to acquire prey.

INTRODUCTION

Toothed whales differ from mysticetes in that they typically pursue, capture, and swallow single prey rather than filter out numerous prey items simultaneously. The morphological adaptations and foraging behavior that have evolved relating to feeding vary greatly among odontocetes. Most species have supernumerary teeth and a secondarily homodont dentition that is used to pierce and hold the prey of odontocetes: fish and/or squid (Norris and Mohl, 1983; Heyning, 1989a). Oceanic dolphins (Delphinidae) of the genera *Stenella* Gray, 1866 and *Delphinus* Linnaeus 1758 may have as many as 200 teeth (Leatherwood et al., 1988:216) within long, slender snouts, which have been referred to as pincer-type jaws by Norris and Mohl (1983).

The beaked whales (Family Ziphiidae) are characterized by the numerical reduction of erupted teeth. Only in one extant species, Shepherd's beaked whale (*Tasmacetus shepherdi* Oliver, 1937), does a full complement of teeth erupt in both jaws (Mead, 1989a). In all other extant species, only one or two pairs of mandibular teeth erupt at sexual maturity. In both Arnoux's and Baird's beaked whales (genus *Berardius* Duvernoy, 1851), two pairs of apical teeth erupt in both sexes. In Cuvier's beaked whale (*Ziphius cavirostris* Cuvier, 1823), both species of bottlenose whales (genus *Hyperoodon* Lacépède, 1804), and all 13 species of *Mesoplodon* Gervais, 1850, only one pair of teeth erupts in sexually mature males.

All extant species of ziphiids possess at least one pair of anteriorly converging throat grooves (Heyning, 1989a). Some specimens of Baird's beaked whale (*Berardius bairdii* Stejneger, 1883) may have accessory throat grooves (Omura et al., 1955).

Ziphiids are often described as primarily squid-eaters (e.g., Gaskin, 1982; Clarke, 1986), however, they also may consume large quantities of fish and/or other invertebrates (Mead, 1989a,b,c; Reyes et al., 1991; Heyning, 1989b; Balcomb, 1989).

Thus, how do these functionally edentulous odontocetes capture their prey? We tested the hypothesis that ziphiids capture their prey primarily by means of suction.

It has been suggested that many other groups of odontocetes use suction as a means to acquire food items (Caldwell et al., 1966; Norris and Mohl, 1983; Brodie, 1989). Several authors have suggested that the tongue is employed in a piston-like manner to produce suction in order to capture prey items (Caldwell et al., 1966; Norris and Mohl, 1983), although none provided evidence that this occurs. Lawrence and Schevill (1965) provided detailed anatomical descriptions of delphinid gular musculature but limited their functional interpretations to the laryngeal region. An analysis of suction feeding within certain delphinoid cetaceans is in progress by Werth (1989, 1991).

For suction feeding to occur, some mechanism must allow the intraoral pressure to drop relative to that of the surrounding water (Lauder, 1985). This would require an increase in volume of the oral and/or pharyngeal cavities. Therefore, we

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Table 1. Specimens examined for this study. Institutional acronyms are: LACM, Natural History Museum of Los Angeles County; USNM, National Museum of Natural History; CAS, California Academy of Sciences.

Species	Sex	Length	Specimen number
SPECIMENS DISSECTED			
Ziphiidae			
Berardius baridii	M	10.30	LACM 86029
	M	10.10	LACM 86033
	M	10.55	LACM 86030
	M	9.50	LACM 86031
	F	?	field #91-21
Mesoplodon densirostris	M	2.72	USNM 571325
	M	4.20	USNM 550754
Mesoplodon europaeus	M	3.44	USNM 571354
Mesoplodon mirus	M	4.50	USNM 571357
Mesoplodon stejnegeri	M	2.32	LACM 84299
Delphinidae			
Orcinus orca	M	6.65	LACM 84249
	F	4.50	LACM 84291
Tursiops truncatus	M	3.17	LACM 84269
Grampus griseus	F	3.06	LACM 84298
Delphinus delphis	M	1.91	LACM 86000
Balaenopteridae			
Balaenoptera acutorostrata	?	?	USNM 571487
Balaenoptera physalus	?	?	USNM 571762
LIVE SPECIMENS OBSERVED			
Ziphiidae			
Mesoplodon carlhubbsi	M	2.87	CAS 23751
	M	2.99	CAS 23122
Ziphius cavirostris	F	3.25	released alive

asked the following series of questions: Are the throat grooves distensible? Does the tongue function as a piston, and if so, what muscles enable it to do so? Is the arrangement of the muscles and/or hyoid apparatus different in suction versus nonsuction feeders? We also noted any observational data that support the hypothesis of suction feeding.

MATERIALS AND METHODS

We dissected a series of nonpreserved heads from ziphiids (Table 1) to ascertain both gross and functional morphology. Dissections varied in technique, with some progressing from superficial to deep and others from deep to superficial. These dissections focused on the morphology of the musculature, connective tissue, and bone. A series of delphinid and baleen whale (Balaenopteridae) heads was also dissected for comparative purposes. Dissections were documented by photographs, illustrations, and video recordings. One specimen of the Bering Sea beaked whale (*Mesoplodon stejnegeri* True, 1885, LACM 84299) was serially scanned by Computer Assisted Tomography (CAT) to provide three-dimensional orientations of anatomical structures. For anatomical structures, we followed the nomenclature of Lawrence and Schevill (1965).

To test whether or not the hyoid apparatus differs between ziphiids and delphinids, we measured the maximum length, width, and thickness of the thyrohyoid bones from a series of specimens. The thyrohyoid was chosen because it is the site of attachment for the *sternohyoideus* and *hyoglossus* muscles (Lawrence and Schevill, 1965). We included only those species of delphinids that we suspected do not use suction feeding to any great extent because they possess either numerous teeth and have pincer-type jaws (bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821) and short-beaked common dolphin, *Delphinus delphis* Linnaeus, 1758) or consume relatively large prey that cannot be easily sucked in (e.g., killer whale, *Orcinus orca* (Linnaeus, 1758) and false killer whale, *Pseudorca crassidens* (Owen, 1846)). In addition, the total lengths for the specimens of *Orcinus* and *Pseudorca* approximated or exceeded the total lengths for the beaked whale specimens of *Ziphius* and *Mesoplodon*. This overlap in total length compensates for any allometric scaling in the hyoid bones.

To test whether intraoral volume can be increased, we measured the volume of the oropharynx for an adult Antillean beaked whale (*M. mirus* True, 1913, USNM 571357). Volume measurements were made by suturing closed the esophagus at the level of the occipital condyles and filling the oral cavity with water. We assumed that at rest, the oral cavity and esophagus are a potential space. Thus, measurements should approximate a minimum volume of fluid the animal could potentially draw in during suction feeding. We also manipulated anatomical structures, such as the tongue, in planes parallel to different muscle groups to determine what effects contractions of these muscles might evoke.

Measurements of the maximum gape were collected

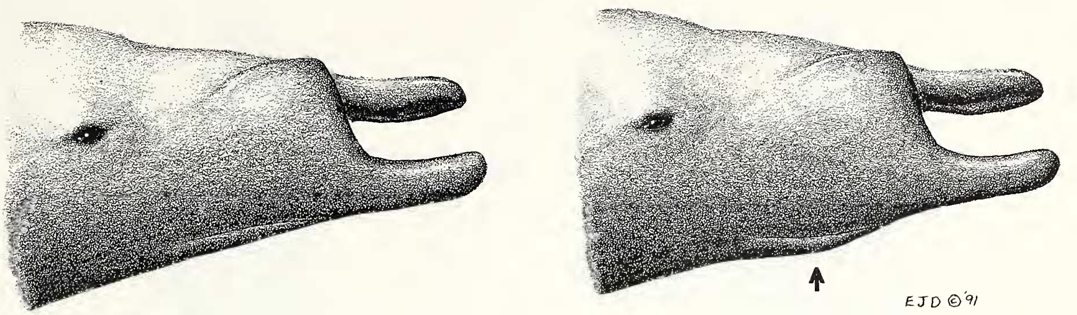

Figure 1. Right lateral view of an adult male *Mesoplodon densirostris* (USNM 550754) showing the relaxed state (left) and the distended state (right) of the gular region by expansion (arrow) of throat grooves. Distension was done manually and probably does not represent the maximum possible in a living ziphiid.

from ziphiids and delphinids, including the maximum extent of jaw opening on a series of specimens of Baird's beaked whale, *B. bairdii.* The gape was measured from the tip of the upper jaw to the tip of the lower jaw as the jaws were opened by an electrical winch. The amount of force exerted in this manner would presumably represent the maximum opening of the mouth without possible tissue damage.

In two instances we studied live-stranded beaked whale calves that were temporarily held in captivity. In the first instance, the gular region on two calves of Hubb's beaked whales, *M. carlhubbsi* Moore, 1963, was palpated to determine if the throat grooves are distensible; we also palpated the oral cavity of the calves to determine if suction could be detected. In the second instance, a series of video recordings were taken of a young stranded female Cuvier's beaked whale, *Z. cavirostris.* The tips of the heads of whole fishes were placed into the gape of this beaked whale, and feeding was recorded. Using stop-frame analysis, the elapsed time from when the fish began to move into the oral cavity until it disappeared completely into the mouth could be documented.

RESULTS

FUNCTIONAL MORPHOLOGY AND OBSERVATIONS

We found that in the species of ziphiids examined the throat grooves are situated between the mandibular symphysis and the hyoid apparatus. In species with a long mandibular symphysis, such as the strap-toothed whale (*M. layardii* (Gray, 1865)), the anterior termini of the throat grooves are situated relatively farther posterior to the tip of the lower jaw than in those species that have a short symphysis, such as *M. mirus* (see Mead, 1989c: figs. 11, 12).

Both live-stranded *M. carlhubbsi* calves exhibited a strong sucking response when either feeding upon fish or suckling on a finger. When this sucking action was being produced, most of the movement detectable by external palpation was in the region of the throat grooves. This region was actively expanded and contracted by muscular activity. Only during respiration was movement detected caudal to the hyoid apparatus. When suckling on a finger, these calves used their tongues to maneuver the finger to the roof of the mouth and hold it there. The frayed anterior and lateral margins of the tongue assisted in forming a tight seal around the finger for suckling.

During dissections, the tongue could easily be retracted posteriorly toward the hyoid apparatus by manipulation. The tongue could move fore and aft smoothly over a loose connective tissue interface between the *geniohyoideus* muscle and the extrinsic tongue muscles (*genioglossus, styloglossus, hyoglossus*) (Fig. 2). The region of the throat grooves was distended when the tongue was retracted. This distension increased when moderate pressure was applied by hand to the floor of the mouth (Fig. 1).

Anterior and lateral to the tongue, the floor of the mouth possesses numerous folds when the tongue is situated in its relaxed, forward position (Fig. 3). When the tongue is retracted, these folds unfurl like pleats. When relaxed, the dorsal surface of the tongue is slightly concave. This shape approximately corresponds with that of the convex palate. Retracting the tongue by manipulation causes the medial surface of the tongue to depress and the lateral edges to turn dorsally: the tongue becomes U-shaped in transverse section.

The mouths of ziphiids can only be opened to a limited extent (Fig. 4). For example, we measured a maximum gape of 7 cm for the adult *M. mirus* we examined. In the sample of 19 *B. bairdii* whales (9.10 to 10.75 m total lengths), the jaws could be opened from 17 to 34 cm with an average of 28 cm.

The oral cavity and esophagus of the adult male *M. mirus* held 1.71 liters. This measure did not include any tongue retraction.

The fish placed into the mouth of the young, live *Z. cavirostris* would remain motionless within the mouth for several seconds. The fish was then drawn into the mouth almost instantly, without any noticeable movement of the whale's head from a dorsolateral view. The elapsed time from when the fish

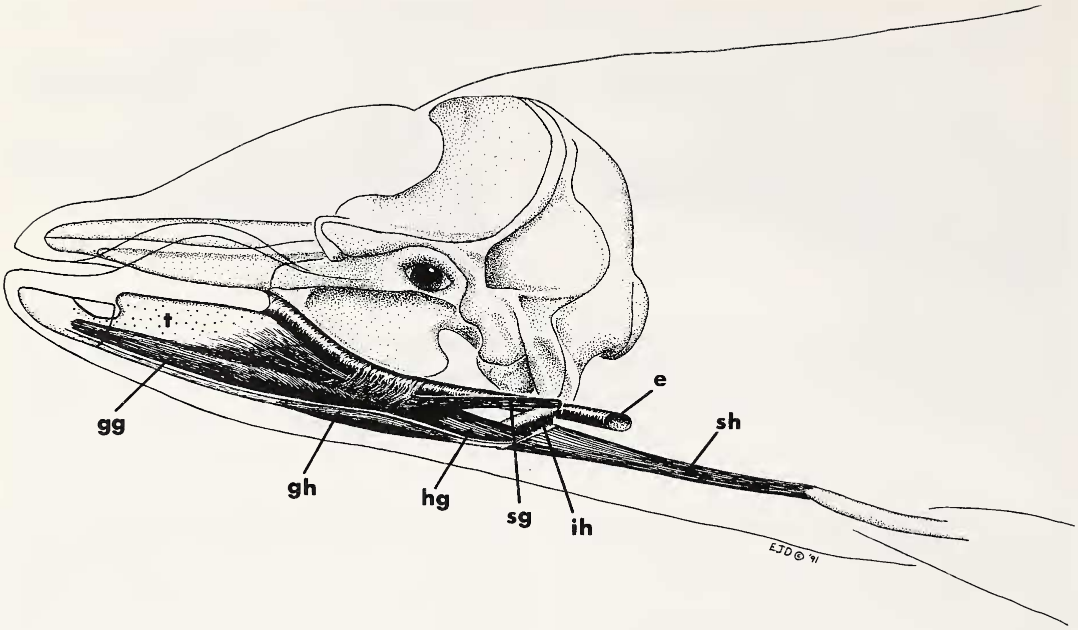

Figure 2. Left lateral diagram of a *Mesoplodon stejnegeri* calf (LACM 84299) showing the orientation of selected gular muscles (e = esophagus, gg = *genioglossus*, gh = *geniohyoideus*, hg = *hyoglossus*, ih = *interhyoideus*, sg = *styloglossus*, sh = *sternohyoideus*, t = tongue).

began to move until it was completely within the oral cavity ranged between one and two frames on the video recording (less than 0.08 seconds).

ANATOMICAL DESCRIPTIONS OF BEAKED WHALE GULAR REGION

The *sphincter colli* is external to the *mylohyoideus* and is clearly separated from this underlying muscle posteriorly as these two muscles are divided by the *digastricus*. In the region of the throat grooves, the *sphincter colli* has transversely oriented fibers that originate from connective tissue just lateral to the throat grooves.

The *mylohyoideus* is found entirely anterior to the hyoid bones. The *mylohyoideus* originates posteriorly from the pterygoid hamuli and/or from along a membrane extending from the hamuli that form the outer surface of the pterygoid sinus. Anteriorly, the *mylohyoideus* adheres to the *geniohyoideus*. The *mylohyoideus* is about 1 cm thick.

The *geniohyoideus* originates as a thin, flat tendon on the rostral surface of basihyoid just ventral to the origin of the *hyoglossus*. The origin of this muscle in ziphiids extends along the medial one third of the fused basihyoid/thyrohyoid bones, whereas in the common dolphin the *geniohyoideus* originates only from the anterior horn of the basihyoid. The fleshy body of this muscle has a wide insertion on the mandible posterior to the symphysis beginning approximately one third the ramus length and continues caudally to just posterior to the gape.

The *genioglossus* inserts on the posterior-lateral surface of the tongue and extends along the lateral surface of the tongue. The insertion is primarily along the ventral median raphe of the tongue, but farther posteriorly some fibers extend dorsally over the esophagus and were first thought by us to be a remnant of the palatoglossus.

As in delphinids (Lawrence and Schevill, 1965), the *styloglossus* originates from the ventrolateral surface of the stylohyoid (Fig. 3), not from the styloid process. It extends anteriorly and medially as a rather cylindrical muscle until it fuses with the lateral head of the *hyoglossus*.

The *hyoglossus* is a thin, broad muscle which originates from the anterior surface of the medial one third of the thyrohyoid. Its origin is deep to the *digastricus* and superficial to the *interhyoideus* muscle. The lateral head of the *hyoglossus* extended about 5 cm anteriorly before fusing with the *styloglossus* in the neonate *M. stejnegeri* we dissected.

The intrinsic muscles of the tongue were quite complex, as is typical for mammals. We did not dissect these muscles in detail.

The *interhyoideus* is a thick, short muscle that is similar to that found in delphinids (Lawrence and Schevill, 1965), except for being relatively larger in ziphiids correlated with the larger hyoid bones.

The *sternohyoideus* is a massive muscle in most cetaceans. In an adult specimen of *M. mirus* the

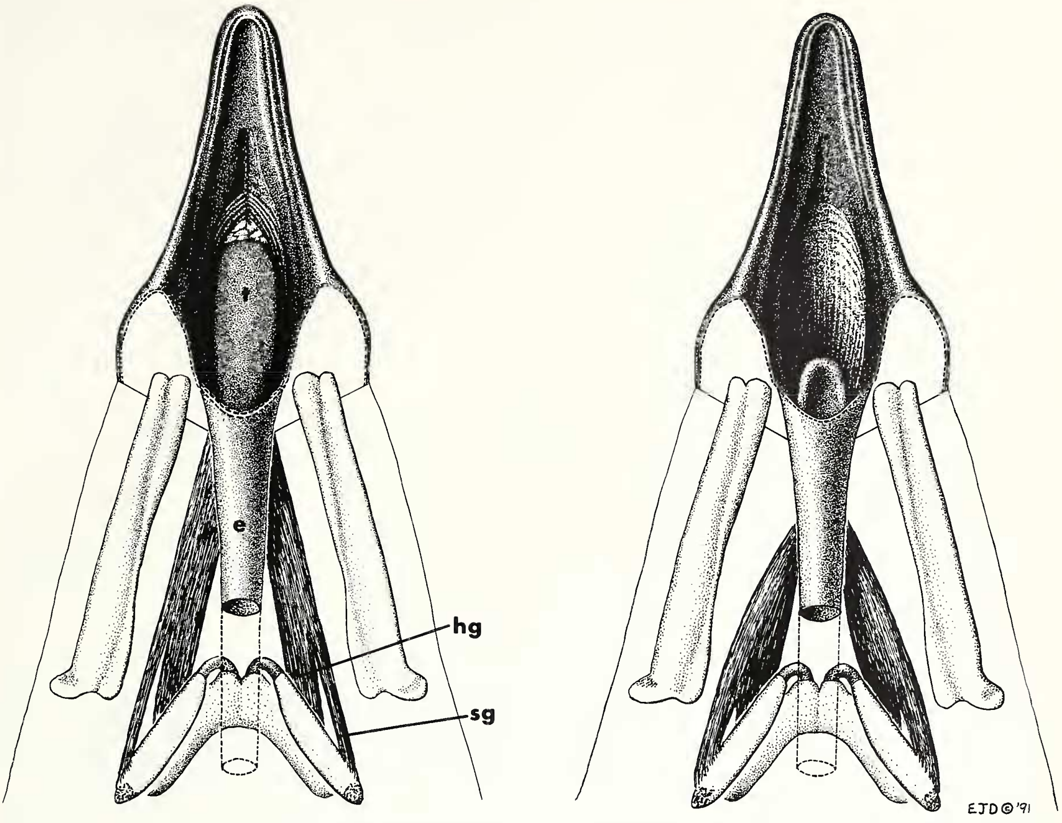

Figure 3. Dorsal diagram of lower jaw and gular muscles of a *Mesoplodon mirus.* The left figure depicts the muscles at rest and figure on right shows tongue retracted by contraction of the *styloglossus* and *hyoglossus* muscles (e = esophagus, hg = *hyoglossus,* sg = *styloglossus,* t = tongue).

midmuscle cross-sectional diameters were 16 by 6 cm. The *sternohyoideus* originates from the anterior margin of the sternum. Near the origin, it is difficult to separate into right and left sides. At approximately midlength, this muscles separates into a bilateral muscle pair. Along the medial surface, about one third the distance to the sternum, there is a connective tissue band that extends medially from the sternum and forms the anterior surface of the thoracic cavity.

The *digastricus* originates as a broad, thin tendon from the anterior margin of the fused basihyoid/thyrohyoid. The belly of this muscle is fleshy near the origin and then becomes more tendinous as it inserts onto the intramandibular fat pad and ventral posterior half of the mandible.

We were unable to locate a *palatoglossus* muscle in any of the specimens of *Mesoplodon* or *Ziphius* dissected.

The fused thyrohyoid and basihyoid bones of beaked whales (Ziphiidae) are relatively wider and thicker than those of dolphins (Delphinidae) (Table 2, Fig. 5). The thyrohyoid/basihyoid complex is the attachment for the *sternohyoideus* as well as most of the extrinsic gular musculature.

DISCUSSION

Many aquatic vertebrates capture prey by suction. Examples include sharks (Tanaka, 1973), numerous groups of actinopterygians, some salamanders and turtles (Lauder, 1985; Lauder and Shaffer, 1986) and walruses (Fay, 1981; Kastelein et al., 1994). Suction is an effective technique of prey acquisition for aquatic predators because of the incompressibility of water.

Several authors have previously alluded to the possibility that several species of odontocetes may use suction to capture food. For example, suction feeding has been suggested for sperm whales (Physeteridae) (Caldwell et al., 1966; Berzin, 1971), beluga whales (Monodontidae) (Ray, 1966:671; Brodie, 1989), and for most extant odontocetes (Norris and Mohl, 1983). Ray (1966:671) observed that captive belugas (*Delphinapterus leucas* (Pallas, 1776)) could suck a 50-cent coin off the bottom from about 4 inches distance. Tomilin and Morozov (1968) noted that captive harbor porpoises (*Phocoena phocoena* (Linnaeus, 1758)) could suck a fish "with some force" from the hand of a trainer at a distance of 3 to 5 cm; they also stated that the

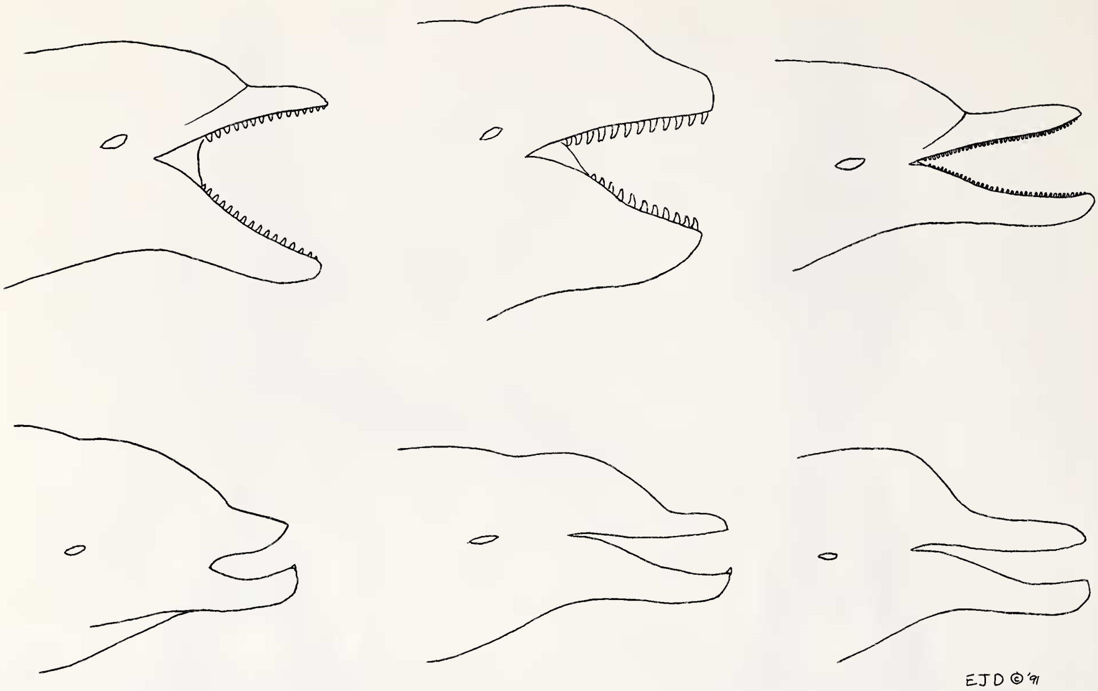

Figure 4. Maximum jaw opening for several species of delphinids (top) and ziphiids (bottom). Clockwise from upper left: *Tursiops truncatus, Orcinus orca, Delphinus delphis, Berardius bairdii, Mesoplodon mirus,* and *Ziphius cavirostris.*

harbor porpoises could suck in dead, drifting fish from at least 10 cm.

THROAT GROOVES

As noted previously, at least one pair of anteriorly converging throat grooves is present in all species of extant ziphiids. Throat grooves of varying number are also found on the sperm whale (*Physeter catodon* Linnaeus, 1758) (Clarke, 1956), on the pygmy sperm whale (*Kogia breviceps* Blainville, 1838), and on some specimens of the dwarf sperm whale (*Kogia simus* (Owen, 1866)) (Caldwell and Caldwell, 1989; unpublished data, LACM and USNM). Several authors (Beddard, 1900; Boschma, 1938; Clarke, 1956) have suggested that the throat grooves of sperm whales and beaked whales function to allow the throat to expand when the animals swallowed large prey. The term "throat grooves" is somewhat of a misnomer as these grooves are situated ventral to the oral cavity and anterior to the hyoid bones, not the esophageal region. Thus, it is unlikely that the distension of the throat grooves could directly facilitate the passing of food down the esophagus in these species.

In the ziphiids we examined, the throat grooves allowed the floor of the oral cavity to be distended ventrally, thus increasing the intraoral volume. The throat grooves of ziphiids are always located posterior to the mandibular symphysis, the region that allows gular distention. We suspect that this may also be the case for sperm whales, as this anatomical region seems to be distended in photographs of some living individuals (e.g., Cousteau and Diole, 1972:135).

The function of throat grooves is better understood for rorqual whales (Balaenopteridae) in which these grooves open like pleats allowing the distension of the oral cavity by the filling of the *cavum ventrale* (Pivorunas, 1977; Lambertsen, 1983; Orton and Brodie, 1987).

Gray whales (*Eschrichtius robustus* (Lilljeborg, 1861)) possess from two to five throat grooves (Andrews, 1914). Andrews (1914) suggested that these grooves may function to allow the gular region to expand during feeding. Observations of a captive juvenile gray whale (Gigi) demonstrated that this species can also generate suction as a method of capturing food prey (Ray and Schevill, 1974). This captive whale was able to suck squid off the bottom in a swath about 30 to 50 cm wide while swimming 10 to 20 cm above the bottom. These authors also noted that the throat grooves allowed for the distention of the floor of the mouth while the whale was drawing in food. This distention is clearly visible in photographs of bottom-feeding wild gray whales (e.g., Simon, 1989:23).

The method by which the gular region is distended in gray whales, sperm whales, and beaked whales probably differs significantly from that of rorqual whales. In the former groups it is likely that active

Table 2. Hyoid bone measurement ratios for beaked whales and selected delphinids.

Species	Sex	Length	LACM number	Hyoid Thickness/ length	Hyoid Width/ length
Ziphiidae					
Berardius bairdii	M	9.50	86031	0.20	0.41
	M	9.50	86032	0.22	0.40
	M	10.10	86033	0.22	0.37
Ziphius cavirostris	F	5.37	88971	0.17	0.43
	M	5.49	84111	0.15	0.44
Mesoplodon carlhubbsi	M	4.96	52437	0.17	0.43
Delphinidae					
Orcinus orca	M	6.65	84249	0.08	0.32
Pseudorca crassidens	M	4.80	84047	0.12	0.33
	M	3.78	84289	0.07	0.30
Tursiops truncatus	M	3.17	84269	0.10	0.35
	M	3.04	84194	0.08	0.35
	F	2.88	88918	0.08	0.25
Delphinus delphis	F	1.81	88926	0.08	0.34

muscular contraction increases the volume of the oral cavity. In rorquals, the mouth is opened while the whale is swimming and thus water pressure passively fills the oral cavity (Orton and Brodie, 1987).

We postulate that after distention, the gular region returns to its resting position primarily as a result of the elastic nature of most of the tissues, especially the blubber and adjacent fascia. In dead specimens, the throat grooves return to their closed state after being manually distended. This type of elastic recoil has been suggested to function similarly in constricting the *cavum ventrale* of rorqual whales (Lambertsen, 1983; Orton and Brodie, 1987). In addition, the muscle fibers of the *sphincter colli profundus* and the *mylohyoideus* are oriented to assist in reducing the intraoral volume by actively constricting the gular region.

TONGUE

The tongue of beaked whales can be retracted in a piston-like manner, as previously suggested for other odontocetes. Because of their anatomical orientation, the *hyoglossus* and *styloglossus* appear to be the primary retractors of the tongue. The increased width and thickness of the hyoid bones in ziphiids provides a greater surface of attachment for these relatively large tongue muscles. This increased surface area of the basihyoid/thyrohyoid bones in ziphiids also serves as the attachment of the relatively massive *sternohyoideus* (*contra* Reidenberg and Laitman, 1994). Only sperm whales (both *Physeter* and *Kogia*) have relatively larger hyoids. The hyoid apparatus is an important functional component for suction feeding in vertebrates (Lauder, 1985). On a dissected head, when the tongue is retracted manually, it inherently becomes shorter longitudinally but thicker in cross-section. If this is not a postmortem artefact, this may allow the tongue to form a tight seal against the walls and roof of the mouth as the tongue is retracted, thereby creating a more efficient piston. The insertion of the *genioglossus* facilitates tongue retraction because it inserts along the posterolateral aspect of the tongue. By not attaching to the rostral aspect of the tongue, the *genioglossus* does not impede tongue retraction or result in the over-stretching of the fibers of this muscle.

Other odontocetes may be able to retract their tongues to varying degrees. Donaldson (1977:194) stated that in *Tursiops* the tongue could be retracted by the *hyoglossus* and *styloglossus*. He also noted that the tongue became shorter longitudinally and thicker in cross-section. He suggested that the thickened, retracted tongue functioned at least partially to occlude the esophagus, thus preventing water from entering the esophagus during prey acquisition. Sonntag (1922) wrote that the tongue of the blunt-headed delphinid *Orcella* Gray, 1866, was quite mobile, whereas the tongue of the extremely long-beaked river dolphin *Platanista* Wigler, 1830, exhibited very restricted movement. This observation corroborates the idea that blunt-headed delphinids may employ suction feeding whereas long-snouted species with a very high tooth count do not.

All neonate and young juvenile ziphiids we examined possessed marginal papillae on their tongues. These marginal papillae have been demonstrated to regress in size with age in delphinids and phocoenids (Donaldson, 1977; Kastelein and Dubbeldam, 1990). These latter authors speculated that these papillae function to assist the tongue in forming a tighter seal while nursing, and later in life may assist in holding prey against the palate while letting water escape between the papillae.

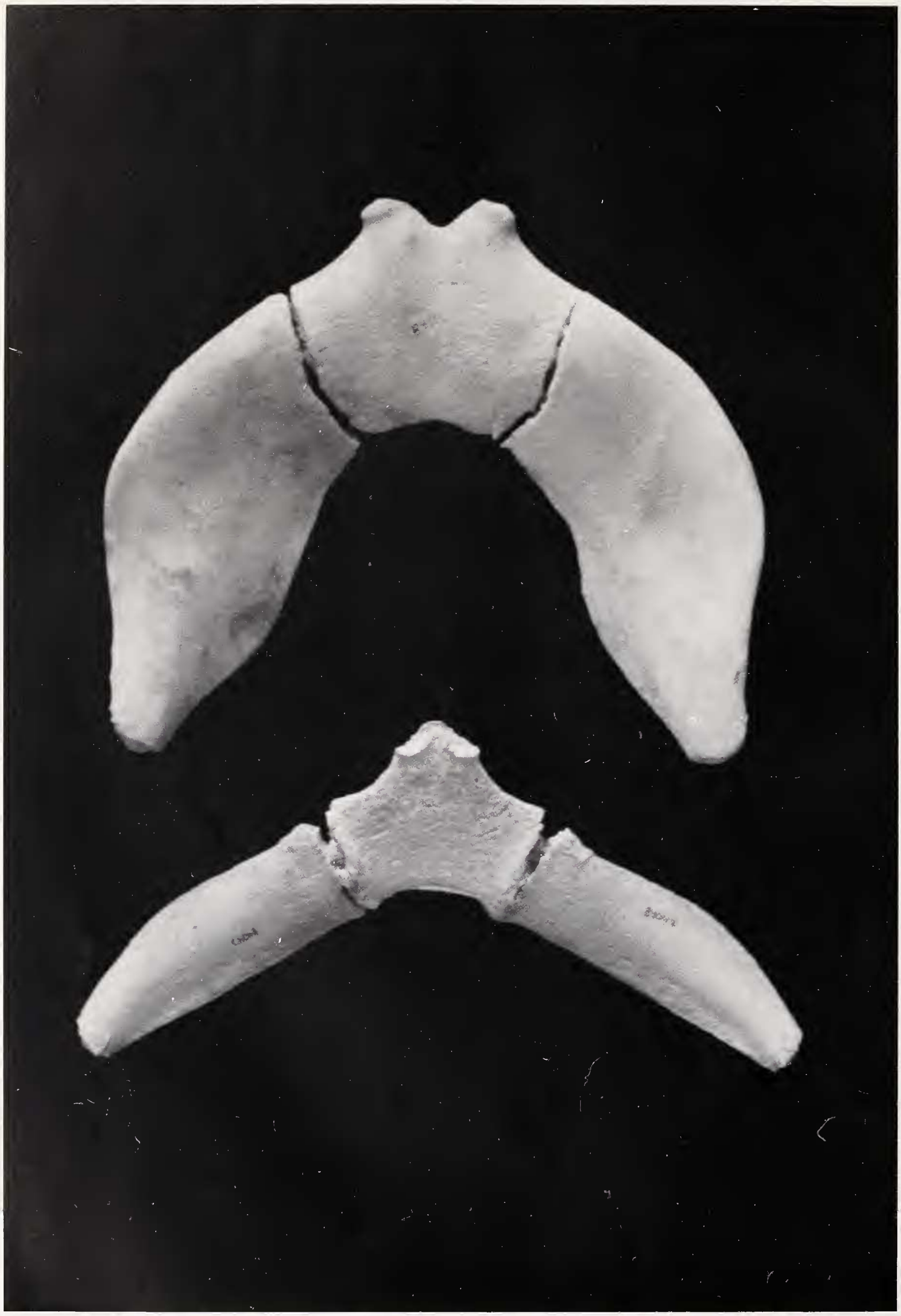

Figure 5. Dorsal views of the fused basihyoid and thyrohyoids of a beaked whale (*Ziphius cavirostris,* LACM 84111), *top,* and a presumed nonsuction-feeding dolphin (*Pseudorca crassidens,* LACM 84047).

The floor of the mouth anterior and lateral to the tongue is deeply pleated in beaked whales. Shallow folds have been recorded in several taxa of odontocetes (Sonntag, 1922; Arvy and Pilleri, 1972; Donaldson, 1977). Arvy and Pilleri (1972) termed these folds the "linguopharygeal grooves." These authors examined these folds for ducts and glands, but did not comment on their function. We found that these pleats unfurl during tongue retraction.

Anteriorly, the *geniohyoideus* consists of a broad, flat tendon that may allow the tongue to slide over it smoothly. In addition, there is a layer of loose connective tissue between the tongue with its extrinsic muscles and the more superficial *geniohyoideus*. It is along this plane that the tongue moves internally. This loose connective tissue layer is similar in construction and function to that of the *cavum ventrale* of rorqual whales (see Lambertsen, 1983). However, the *cavum ventrale* of rorquals allows for significant lateral movement of the gular floor as the tongue inverts during feeding.

In order to enhance gular distention, a ventrally directed force is advantageous. The enlarged pterygoid hamuli found on the skulls of ziphiids extend ventrally quite far compared to those in other cetaceans (Fig. 6). As the tongue is drawn caudally, it also must move ventrally along the pterygoid hamuli. This may create the downward vector needed to expand the throat grooves and thus contribute to increasing the intraoral volume, thereby decreasing the intraoral pressure.

GAPE

Ziphiids are unable to open their mouths very wide. Most species possess a great deal of superficial tissue around the corner of the mouth (Heyning, 1989a). This is particularly true for adult males of the genus *Mesoplodon* in which the teeth are situated more posteriorly along the mandible (Mead et al., 1982). This combination of a small gape and tissue around the corner of the mouth results in a relatively small and somewhat restricted oral opening.

A restricted aperture of the mouth is most efficient for suction feeding, as all the water is drawn in through a relatively small orifice (Alexander, 1967). Belugas are able to purse their lips in order to form a small, round, terminal opening to the mouth for suction feeding (see Brodie, 1989: fig. 5). Tomilin and Morozov (1968) observed that harbor porpoises only opened their mouths about 0.5 to 1 cm when engaging in suction feeding. Therefore, we propose that the limited extent to which ziphiids can open their mouths is an adaptation for suction feeding.

The ziphiid with the most restricted gape is the strap-toothed whale (*M. layardii*). It has been questioned how adult male *M. layardii* feed as their erupted mandibular teeth curve above the snout, thereby limiting the extent to which they can open their mouths (e.g., Ellis, 1980). The measured gapes of an adult female and an immature male strap-toothed whale were markedly wider (6.5 cm) than the gapes of two adult males (3.2 and 4.0 cm), indicating that the erupted teeth do in fact limit the maximum extent to which the mouth can be opened in this species (Sekiguchi et al., 1996). Leatherwood et al. (1983) stated that the erupted teeth of adult males may function as "guide rails" funneling prey into the mouth. Because females and immature males lack such guide rails, it is more reasonable to assume that these teeth function in intraspecific fighting (Heyning, 1984). Both male and female *M. layardii* typically feed on squid significantly smaller (less than 100 g and mantle lengths less than 16 cm) than those fed upon by *Ziphius cavirostris* in spite of the fact that both of these ziphiids are approximately the same size (Sekiguchi et al., 1996). The restricted gape of strap-toothed whales may be an adaptation for sucking in small squid. By specializing on small squid, *M. layardii* may avoid competition for food with sympatric teuthophagous odontocetes such as *Z. cavirostris, Hyperoodon planifrons,* and *Physeter catodon.*

REDUCED TOOTH COUNT

There is a trend for primarily squid eating (teuthophagous) species to exhibit a reduced tooth count (Gaskin, 1982; Clarke, 1986). For those that retain teeth, such as the sperm whale and beaked whales, it has been postulated that these teeth serve more for social interactions than for prey acquisition (Heyning, 1984).

The supernumerary teeth typical of most odontocetes may not be efficient for suction feeding. This is because there is a significant region where water could enter the oral cavity between the teeth, but the sucking in of prey items would be hindered by this dental barrier. The broad-headed delphinoid species with reduced dentition, such as *Grampus* Gray 1828, *Globicephala* Lesson, 1828, and *Delphinapterus,* which are teuthophagous, lack teeth at the extreme terminus of the mouth where prey would be sucked in. It has been previously noted that most species of ziphiids lack erupted teeth. We hypothesize that a reduction in dentition would be selected for as an advantage in the evolution of suction feeding.

The palates of the ziphiids we examined were rugose with small cornified papillae. We found a similar condition on the palate of the delphinid *Grampus griseus,* a teuthophagous species of delphinid with a reduced tooth count. In Dall's porpoise (*Phocoenoides dalli*), there are small dermal ridges interspersed between the extremely reduced teeth, and the palate is coarsely wrinkled with broad ridges (Miller, 1929). Gaskin (1982) commented that such a rugose palate would facilitate the holding of slippery squid. Such a palate would provide a non-skid surface which does not offer projections (i.e., teeth) upon which the squid's tentacles can grasp and thus hinder the ingestion of the still live prey.

WATER FLOW

Vertebrates with gills have a unidirectional flow of water into the mouth and out from the gills. Higher

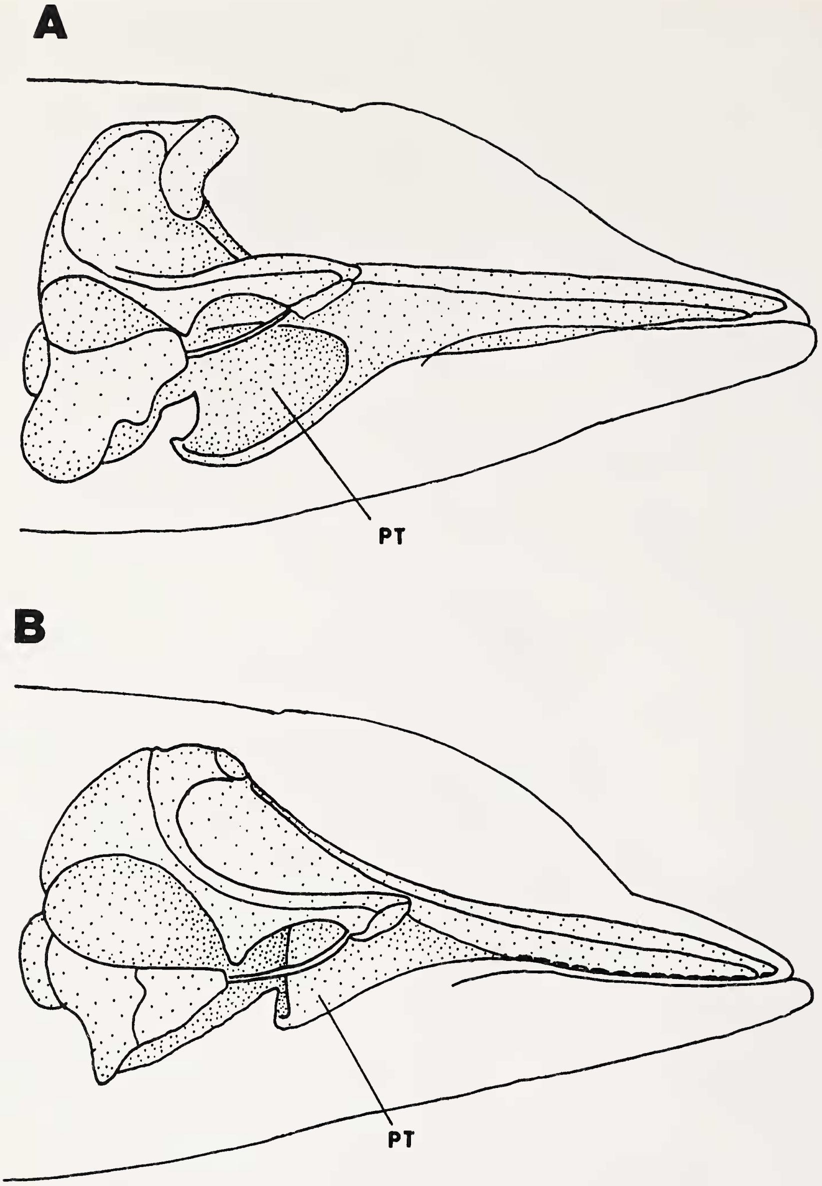

Figure 6. Right lateral diagrammatic view of the skulls and body outline of a beaked whale (A) *Mesoplodon carlhubbsi,* and a dolphin (B) *Tursiops truncatus.* Note the enlarged pterygoid (PT) of the beaked whale compared to the small pterygoid of the dolphin. Illustrations are not to scale.

vertebrates, including adult amphibians, lack gills and thus during suction feeding water flow is bidirectional, both in and out through the mouth. In a study that compared larval and adult tiger salamanders, Lauder and Shaffer (1986) suggested that unidirectional flow was more efficient than the bidirectional flow. Species that employ a bidirectional flow system must hold water while they secure the prey prior to expressing the water out of the mouth. In an unrelated study, Harrison et al. (1970) noted that the forestomach of dolphins can hold up to several liters of water. These authors pointed out that there is no muscular sphincter between the esophagus and forestomach. They also observed dolphins ejecting water from the mouth in such a volume as to suggest that some of this water was coming from the forestomach. It may be possible that one function of the forestomach of odontocetes may be to act as a reservoir for sea water that has been sucked in. We suggest that it is plausible that these odontocetes may hold water in their forestomach while they secure the prey against the rugose palate and then release the water past the secured prey.

PIGMENTATION

Many of the beaked whale species we dissected had white or lightly pigmented epidermis on the anterior floor of the mouth. We hypothesize that this may be an attractant for bioluminescent squid. Previously, Gaskin (1967) hypothesized that the white lower jaws and teeth of sperm whales may retain the bioluminescent bacteria from consumed squid and this in turn may attract additional squid. Other odontocetes (e.g., *Pepenocephala* Nishiwaki and Norris, 1966, *Feresa* Gray, 1870, and *Steno* Gray 1846) also have strikingly delimited white lip patches. However, the white on the tip of the snout of some adult male beaked whales has been suggested to visually enhance the size of the erupted teeth (Heyning, 1984). This particular visual cue may relate more to intraspecific communication than to feeding.

CONCLUSIONS

The throat grooves of beaked whales provide for the distension of the floor of the mouth. The *styloglossus* and *hyoglossus* muscles are the principle tongue retractors. This extensive movement of the tongue is facilitated by a smooth, loose connective tissue layer between the tongue and *genioglossus* muscles. Tongue retraction and gular floor distention results in the expansion of the oral cavity, thereby creating low pressure within the oral cavity and allowing water to be sucked into the mouth. Limited observations show that beaked whales are able to suck in their prey. The ability to echolocate coupled with suction feeding imparts a tremendous advantage to odontocetes foraging in the aphotic zone.

Suction feeding could explain the observations of intact squid found in the stomachs of sperm whales and ziphiids. Previously these prey items, which lack teeth marks, were used as evidence to support the hypothesis that the prey had been stunned by high intensity echolocation sounds (Berzin, 1971; Norris and Mohl, 1983). As noted previously, the primary function of the teeth of sperm whales and beaked whales, as well as some delphinids, is related to intraspecific aggression, not to prey acquisition and processing. Suction feeding by these cetaceans would explain why squid found in the stomach have no teeth marks.

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LITERATURE CITED

Alexander, R. McN. 1967. *Functional design in fishes.* London: Hutchinson and Co. Ltd., 160 pp.

Andrews, R.C. 1914. The California gray whale (*Rhachianectes glaucus* Cope): Its history, habits, external anatomy, osteology and relationship. *Memoirs of the American Museum of Natural History, New Series, vol. 1, part V. Monographs of the Pacific Cetacea,* 227–287.

Arvy, L., and G. Pilleri. 1972. Comparison of the tongues of some odontocetes (*Pontoporia, Neomeris,* and *Delphinus*). *Investigations on Cetacea* 4:191–200 + 6 pls.

Balcomb, K.C., III. 1989. Baird's beaked whale *Berardius bairdii* Stejneger, 1883; Arnoux's beaked whale *Berardius arnuxii* Duvernoy, 1851. In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 261–288. London: Academic Press.

Beddard, F.E. 1900. *A book of whales.* London: John Murray, xv + 320 pp.

Berzin, A.A. 1971. *The sperm whale.* Jerusalem: Israel Program for Scientific Translation (English translation, 1972), v + 394 pp.

Boschma, H. 1938. On the teeth and some other particulars of the sperm whale (*Physeter macrocephalus* L.). *Temminckia* 3:151–278.

Brodie, P.F. 1989. The white whale—*Delphinapterus leucas* (Pallas, 1776). In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 119–144. London: Academic Press.

Caldwell, D.K., and M.C. Caldwell. 1989. Pygmy sperm whale *Kogia breviceps* (de Blainville, 1838): Dwarf sperm whale *Kogia simus* Owen, 1866. In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 235–260. London: Academic Press.

Caldwell, D.K., M.C. Caldwell, and D.W. Rice. 1966. Behavior of the sperm whale, *Physeter catodon* L. In *Whales, dolphins, and porpoises,* ed. K.S. Norris, 677–717. Berkeley: University of California Press.

Clarke, M.C. 1986. Cephalopods in the diets of odontocetes. In *Research on dolphins,* ed. M.M. Bryden and R. Harrison, 281–321. Oxford: Clarendon Press.

Clarke, R. 1956. Sperm whales of the Azores. *Discovery Reports* 28:237–298.

Cousteau, J-Y., and P. Diole. 1972. *The whale: Mighty monarch of the sea.* Garden City, New York: Doubleday and Co., 304 pp.

Donaldson, B.J. 1977. The tongue of the bottle-nosed dolphin (*Tursiops truncatus*). In *Functional anatomy of marine mammals,* vol. 3., ed. R. Harrison, 175–197. London: Academic Press.

Ellis, R. 1980. *The book of whales.* New York: Alfred A. Knopf, xvii + 202 pp.

Fay, F. 1981. Walrus—*Odobenus rosmarus.* In *Handbook of marine mammals,* vol. 1, ed. S.H. Ridgway and R. Harrison, 1–23. London: Academic Press.

Gaskin, D.E. 1967. Luminescence in a squid *Moroteuthis* sp. (probably *ingens* Smith), and a possible feeding mechanism in the sperm whale *Physeter catodon* L. *Tuatara* 15(2):86–88.

Gaskin, D.E. 1982. *The ecology of whales and dolphins.* London: Heineman Education Books Ltd., pagination.

Harrison, R.J., F.R. Johnson, and B.A. Young. 1970. The oesophagus and stomach of dolphins (*Tursiops, Delphinus, Stenella*). *Journal of Zoology, London* 160: 377–390.

Heyning, J.E. 1984. Functional morphology involved in intraspecific fighting of the beaked whale, *Mesoplodon carlhubbsi. Canadian Journal of Zoology* 62: 1645–1654.

Heyning, J.E. 1989a. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. *Contributions in Science* 406:1–65.

Heyning, J.E. 1989b. Cuvier's beaked whale, *Ziphius cavirostris* G. Cuvier, 1823. In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 289–308. London: Academic Press.

Kastelein, R.A., and J.L. Dubbeldam. 1990. Marginal papillae on the tongue of the harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*) and Commerson's dolphin (*Cephalorhynchus commersonii*). *Aquatic Mammals* 15:158–170.

Kastelein, R.A., M. Muller, and A. Terlouw. 1994. Oral suction of a Pacific walrus (*Odobenus rosmarus divergens*) in air and under water. *Zeitschrift für Saugetietrkunde* 59:105–115.

Lambertsen, R.H. 1983. Internal mechanisms of rorqual feeding. *Journal of Mammalogy* 64:76–88.

Lauder, G.V. 1985. Aquatic feeding in lower vertebrates. In *Functional vertebrate morphology,* ed. M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, 210–229. Cambridge, Massachusetts: Harvard University Press.

Lauder, G.V., and H.B. Shaffer. 1986. Functional design of feeding mechanism in lower vertebrates: Unidirectional and bidirectional flow systems in the tiger salamander. *Zoological Journal of the Linnean Society* 88:277–290.

Lawrence, B., and W.E. Schevill. 1965. Gular musculature in delphinids. *Bulletin of the Museum of Comparative Zoology* 133(1):1–65.

Leatherwood, S., R.R. Reeves, and L. Foster. 1983. *The Sierra Club handbook of whales and dolphins.* San Francisco: Sierra Club Books, xviii + 302 pp.

Leatherwood, S., R.R. Reeves, W.F. Perrin, and W.E. Evans. 1988. *Whales, dolphins, and porpoises of the eastern North Pacific and adjacent Arctic waters: A guide to their identification.* New York: Dover Publications, Inc., ix + 245 pp.

Mead, J.G. 1989a. Shepherd's beaked whale *Tasmacetus shepherdi* Oliver, 1937. In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 309–320. London: Academic Press.

Mead, J.G. 1989b. Bottlenose whales *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* Flower, 1882. In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 321–348. London: Academic Press.

Mead, J.G. 1989c. Beaked whales of the genus *Mesoplodon.* In *Handbook of marine mammals,* vol. 4, ed. S.H. Ridgway and R. Harrison, 349–430. London: Academic Press.

Mead, J.G., W.A. Walker, and W.J. Houck. 1982. Biological observations on *Mesoplodon carlhubbsi* (Cetacea: Ziphiidae). *Smithsonian Contributions to Zoology* 344:iii + 1–25.

Miller, G.S. 1929. The gums of the porpoise *Phocoenoides dalli* (True). *Proceedings of the U.S. National Museum* 74:1–4 + pls. 1–4.

Norris, K.S., and B. Mohl. 1983. Can odontocetes debilitate prey with sound? *American Naturalist* 122:85–104.

Omura, H., K. Fujino, and S. Kimura. 1955. Beaked whale *Berardius bairdi* of Japan with notes on *Ziphius cavirostris. Scientific Reports of the Whales Research Institute* 10:89–132.

Orton, L.S., and P.F. Brodie. 1987. Engulfing mechanics of fin whales. *Canadian Journal of Zoology* 65: 2898–2907.

Pivorunas, A. 1977. The fibrocartilage skeleton and related structures of the ventral pouch of balaenopterid whales. *Journal of Morphology* 151:299–314.

Ray, G.C. 1966. *Comment in* Round Table: Practical Problems. In *Whales, dolphins, and porpoises,* ed. K.S. Norris, 649–673. Berkeley: University of California Press.

Ray, G.C., and W.E. Schevill. 1974. Feeding of a captive gray whale, *Eschrichtius robustus. Marine Fisheries Review* 36(4):31–38.

Reidenberg, J.S., and J.T. Laitman. 1994. Anatomy of the hyoid apparatus in Odontoceti (toothed whales): Specializations of their skeleton and musculature compared with those of terrestrial mammals. *The Anatomical Record* 240:598–624.

Reyes, J., J.G. Mead, and K. van Waerebeek. 1991. A new species of beaked whale *Mesoplodon peruvianus* sp. n. (Cetacea: Ziphiidae) from Peru. *Marine Mammal Science* 7:1–24.

Sekiguchi, K., N.T.W. Klages, and P.B. Best. 1996. The diet of strap-toothed whales (*Mesoplodon layardii*). *Journal of Zoology* 239:453–463.

Simon, S. 1989. *Whales.* Trophy (Harper Collins Children's Division) New York, v. + 40 pp. (unpaginated).

Sonntag, C.F. 1922. The comparative anatomy of the tongues of the Mammalia, VII Cetacea, Sirenia and Ungulata. *Proceedings of the Zoological Society of London* 1922: 639–657.

Tanaka, S.K. 1973. Suction feeding by the nurse shark. *Copeia* 1973:606–608.

Tomilin, A.G., and D.A. Morozov. 1968. Sucking in of food—A previously unknown method of *Phocoena phocoena* feeding. *Trudy Vsesoyuznogo Sel'skokhozyaystvennogo Instituta Zaochnogo Obrazovaniya* 31:201–202 (in Russian).

Werth, A.J. 1989. Suction feeding in odontocetes: Water flow and head shape. *American Zoologist* 29(4):92A.

Werth, A.J. 1991. Suction feeding in pilot whales: Kinematic and anatomical evidence. *American Zoologist* 31(5):17A.

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